

# Distribution and Population Development of *Nasonovia ribisnigri* (Homoptera: Aphididae) in Iceberg Lettuce

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**ABSTRACT** A field study was conducted to determine the distribution and development of aphid *Nasonovia ribisnigri* (Mosley) (Homoptera: Aphididae) populations in iceberg lettuce, *Lactuca sativa* L. 'Salinas'. Lettuce plants were transplanted and caged individually in the field and inoculated with apterous *N. ribisnigri* at 0, 1, 2, 3, and 4 wk after transplanting in spring and fall 2002. Plants were harvested 15–50 d after inoculations; numbers of alates and apterous *N. ribisnigri* were counted or estimated on each leaf for each plant. Inoculations during all 5 wk of plant development resulted in successful colonization of lettuce heads. Results indicated that head formation did not reduce the risk of colonization by *N. ribisnigri* to iceberg lettuce; plants were susceptible to colonization by *N. ribisnigri* throughout their development. For later inoculations, *N. ribisnigri* populations were relatively smaller, and aphids were found mostly within the heads. For earlier inoculations, *N. ribisnigri* populations were larger, and within-plant distributions shifted toward frame leaves. The shift of population distributions toward frame leaves correlated significantly with increases in *N. ribisnigri* population density. For most inoculations, more aphids were present on wrapper leaves than on other leaves. The proportion of alates did not vary significantly with population density. Population development of *N. ribisnigri* also correlated significantly with heat unit accumulation. Yellow sticky cards were used to monitor alates in each cage. Catches of *N. ribisnigri* alates on yellow sticky cards were significantly correlated with total numbers of alates as well as with total population sizes on individual lettuce plants.

**KEY WORDS** *Nasonovia ribisnigri*, lettuce, distribution, population development

THE APHID *Nasonovia ribisnigri* (Mosley) (Homoptera: Aphididae) is a major pest of lettuce in western Europe and Canada (Mackenzie and Vernon 1988, Mackenzie et al. 1988, Martin et al. 1995, Rufingier et al. 1997, Ryder 1999). Recently, it was also found in New Zealand (Teulon and Stufkens 2002, Stufkens and Teulon 2003). In the United States, *N. ribisnigri* has become a major pest of lettuce in California and Arizona since its first detection in Salinas Valley in 1998 (Chaney 1999, Palumbo 2000, Palumbo and Hannan 2002). *N. ribisnigri* prefers to feed in the "heart" of lettuce plants, and it is difficult to control with contact insecticides. Lettuce contaminated with *N. ribisnigri* is unmarketable. *N. ribisnigri* is also a vector of virus diseases, including cucumber mosaic virus and lettuce mosaic virus (Davis et al. 1997), although transmission of lettuce mosaic virus in California has not been reported.

Most previous studies on this pest focused on host plant resistance and the development of resistant lettuce cultivars (Eenink and Dieleman 1982, van Helden 1993, van Helden et al. 1992, Ryder 1999, Palumbo and Hannan 2002). Studies on the ecology and behavior of

this pest are limited (Mackenzie and Vernon 1988; van Helden et al. 1992, 1993; Palumbo 2000, 2003; Palumbo and Hannan 2002). Mackenzie and Vernon (1988) reported distributions of *N. ribisnigri* in the field and within lettuce plants. Within head lettuce, *N. ribisnigri* was found mostly on wrapper leaves; small proportions of populations were found on frame leaves and head leaves after *N. ribisnigri* had developed for >45 d on the plants (Mackenzie and Vernon 1988).

For iceberg lettuce, *Lactuca sativa* L. 'Salinas' heart leaves that *N. ribisnigri* prefer to feed on are head leaves inside lettuce heads, shielded by wrapper leaves as plants develop heads. There is no published information regarding the potential for head development to affect susceptibility of lettuce plants to colonization by *N. ribisnigri*. Such information could be used to determine whether there is a time window when iceberg lettuce plants are more susceptible to colonization by *N. ribisnigri*. In the current study, field experiments were conducted to determine colonization success, population distribution, and development in head lettuce after lettuce plants were inoculated with *N. ribisnigri* at different times of plant development.

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## Materials and Methods

**Plants.** Seeds of iceberg lettuce, *Lactuca sativa* L. 'Salinas', were sowed in potting soil in transplanting trays with 3.8 by 3.8 by 5.1 cm (length by width by depth) cells in a greenhouse. Five weeks later, lettuce seedlings were at four-leaf stage and were transplanted in a field plot at USDA Research Station in Salinas, CA. Plants were spaced 0.91 m apart in single rows on standard double row beds. Transplanting was carried out in the spring (28 May) and fall (23 September) 2002. In total, 150 plants were transplanted each time. Plants were fertilized with ammonium sulfate mixed in soil at a rate of 56 kg/ha in the spring and 1 teaspoon of slow-release fertilizer formula Osmocote (24-4-8, N-P-K) added underneath the roots of each plant during the transplanting. The field plot was drip irrigated twice each week. Plants were at early rosette stage  $\approx 3$  wk after transplanting and started to form heads 4 wk after transplanting.

**Insects.** *N. ribisnigri* colonies were established from field-collected individuals in the Spence field in Salinas in 2001. They were reared on romaine *Lactuca sativa* L. 'Valmaine' and iceberg lettuce plants in screen cages (0.91 by 0.91 by 0.91 m) in the greenhouse. New plants were provided for continuous aphid colonization and old and heavily infested plants were removed periodically to maintain the colonies. Plants were watered daily.

**Field Experiment.** One day after transplanting,  $\approx 100$  plants were randomly chosen and caged individually. Each cage was a 38.1 by 38.1 by 38.1 cm (length by width by height) screen bag suspended over a frame formed by two  $\Pi$ -shaped metal rods anchored 38.1 cm apart in parallel in soil over a plant. The screen bag was secured to the frame with binders.

Each week starting 1 d after transplanting,  $\approx 10$  caged plants were chosen randomly from healthy plants and inoculated with apterous *N. ribisnigri*. Abnormally small, diseased, or damaged plants were excluded from the study. Each plant was inoculated only once. Five separate inoculations were conducted during five consecutive weeks to have lettuce plants inoculated with aphids at different times of plant development. Inoculation was accomplished by transferring five medium-large sized apterous *N. ribisnigri* aphids on an infested lettuce plant from *N. ribisnigri* colonies to a caged plant with a soft brush. When plants were small and had not developed heads, insects were placed directly in the hearts of plants. After plants had developed heads, insects were placed on surfaces of wrapper leaves. Cages were opened for insect inoculation and closed immediately after inoculation. Two weeks after inoculation, a yellow sticky card (7.6 by 12.7 cm) (Olson Products, Medina, OH) attached to a 31-cm wood stick with a binder was posted in each cage next to the caged lettuce plant to catch alates of *N. ribisnigri*. *N. ribisnigri* alates on each card were recorded, and the card was replaced each week until lettuce plants were harvested. A magnifying glass was used to assist with identification of *N. ribisnigri*.

Inoculated lettuce plants were harvested during 17–19 July for the spring transplanting and on 13 November for the fall transplanting to determine distribution and size of *N. ribisnigri* populations on individual lettuce plants. Four and three plants for each inoculation time were harvested for the spring and fall transplanting, respectively, to determine distributions and numbers of *N. ribisnigri* within each plant, with one exception of three plants for the first inoculation of the spring transplanting. Plants were selected randomly from inoculated plants after exclusion of plants with abnormally smaller sizes, symptoms of decay, severe head deformation, or the lowest trap catches of *N. ribisnigri* alates within each inoculation time. In total, 34 inoculated lettuce plants were harvested.

By the time of harvest, *N. ribisnigri* had developed for 43, 36, 29, 22, and 15 d, respectively, for the spring transplanting and for 50, 43, 36, 29, and 22 d, respectively, for the fall transplanting. Lettuce plants also became slightly over mature by the time of harvest judged by appearance of plants and compactness of heads. At harvest, numbers of *N. ribisnigri* on both sides of each leaf were counted and recorded starting from the outermost frame leaf toward the center of lettuce heads. Numbers of alates and apterous aphids also were recorded separately for each leaf. When the number of aphids on a leaf surface was judged to be small ( $<100$ ), all aphids were counted individually. For higher densities ( $>100$  per leaf surface), the leaf surface was visually divided into two or more smaller sections based on the appearance of similar numbers of aphids. Aphids in one of the sections were counted in groups of five, and the total number of aphids on the leaf surface was estimated. Weights of lettuce plants also were measured individually on an electronic balance.

**Data Analysis.** Aphid density per unit weight of plant tissue was calculated for all lettuce plants. Proportions of alate population and the total population on frame leaves were correlated with population density to determine relationships between population density and distributions of alates and total aphid populations (PROC REG, SAS Institute 1999). Maximum and minimum air temperature records from the North Salinas weather station (#89) during the experiments were downloaded from the California Irrigation Management Information System (<http://www.cimis.water.ca.gov/>). Heat unit accumulations in degree-days (DD) were calculated from the dates of inoculation of plants with *N. ribisnigri* to the dates of harvest by using a Web-based degree-day calculator of the University of California Statewide Integrated Pest Management System (<http://www.ipm.ucdavis.edu/weather/ddretrieve.html>). A threshold of 5°C and the single-sine method (Wilson and Barnett 1983) were chosen for degree-day calculations. Population sizes of *N. ribisnigri* on individual plants were transformed by logarithm and correlated with degree-days accumulated between inoculation dates and dates of lettuce harvest. Catches of *N. ribisnigri* alates on yellow sticky cards in the final week before harvest also were analyzed for correlation with total population size and

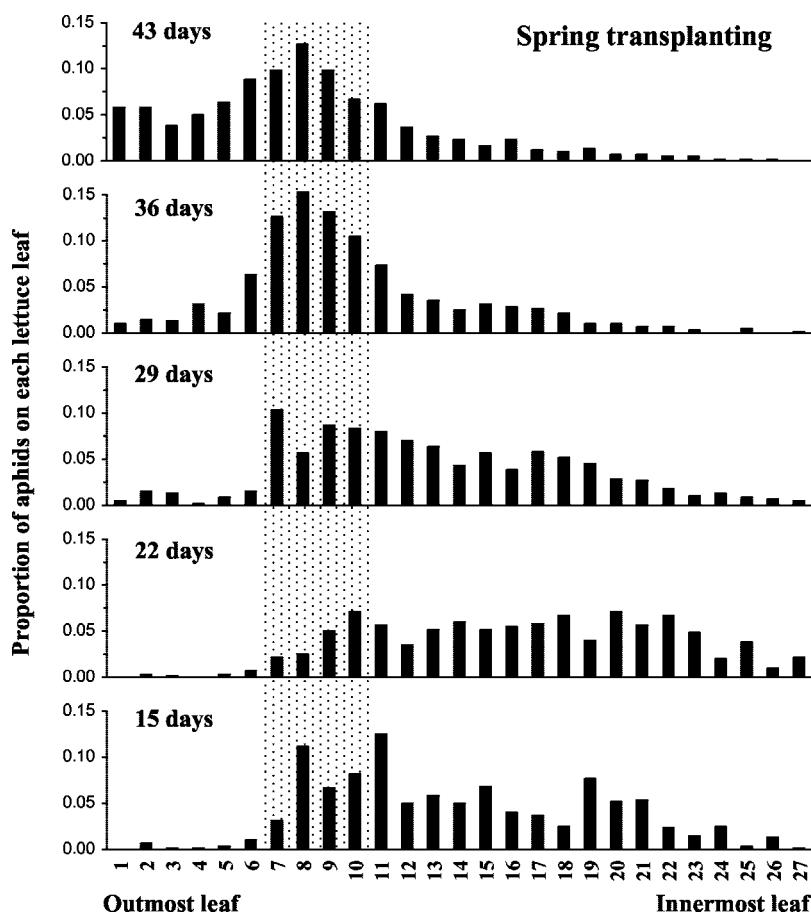


Fig. 1. Distribution of *N. ribisnigri* on leaves of iceberg lettuce plants for spring transplanting. Lettuce plants were transplanted on 28 May 2002 and harvested during 17–19 July 2002. The time period on each graph reflects the developmental time of the *N. ribisnigri* colony by the time of harvest. Leaves were numbered from the outermost frame leaf to the innermost head leaf inspected. Leaves in the shaded area are wrapper leaves.

alate population size of *N. ribisnigri* on individual lettuce plants (PROC REG, SAS Institute 1999).

### Results

Iceberg lettuce plants were susceptible to colonization by *N. ribisnigri* throughout their development. *N. ribisnigri* established colonies for all inoculation dates of both spring and fall transplants. Distributions of *N. ribisnigri* within lettuce plants varied with transplanting time and inoculation time (Figs. 1 and 2). For the spring transplanting, 15 and 22 d after inoculations, aphids were found mostly on head leaves, and only small portions were found on frame leaves. Distributions of *N. ribisnigri* populations shifted toward wrapper leaves and frame leaves as developmental time increased from 29 to 43 d after inoculation (Fig. 1). For the fall transplanting, distributions of *N. ribisnigri* populations showed a similar shift to frame leaves with developmental time. However, for all five *N. ribisnigri* developmental periods in the fall, larger numbers of *N. ribisnigri* were found on wrapper leaves than on heart or frame leaves (Fig. 2). By the last inoculation

15 d before harvest for the spring transplanting, and 22 d before harvest for the fall transplanting, lettuce plants had well formed heads. The distribution of aphids throughout heads for all inoculations indicated that formation of heads did not hinder colonization of iceberg lettuce by *N. ribisnigri*.

Mean population size of *N. ribisnigri* per plant ranged from 287 at 15 d after inoculation to  $\approx 4,000$  at 43 d after inoculation for spring transplanting. It ranged from 212 at 22 d after inoculation to  $\approx 4,000$  at 50 d after inoculation for fall transplanting (Table 1). The ranges of the proportion of aphids on frame leaves, wrapper leaves, and head leaves were 0.02–0.36, 0.17–0.52, and 0.25–0.81, respectively, for spring transplanting. For fall transplanting, the ranges of the proportion of aphids on frame leaves, wrapper leaves, and heads leaves were 0.06–0.40, 0.49–0.69, and 0.10–0.46, respectively (Table 1). Based on population size and the proportion of the population in lettuce heads, the numbers of aphids in lettuce heads ranged from  $\approx 200$  to  $\approx 1000$  for spring transplanting and from 82 to  $>400$  for fall transplanting. The proportion of aphids

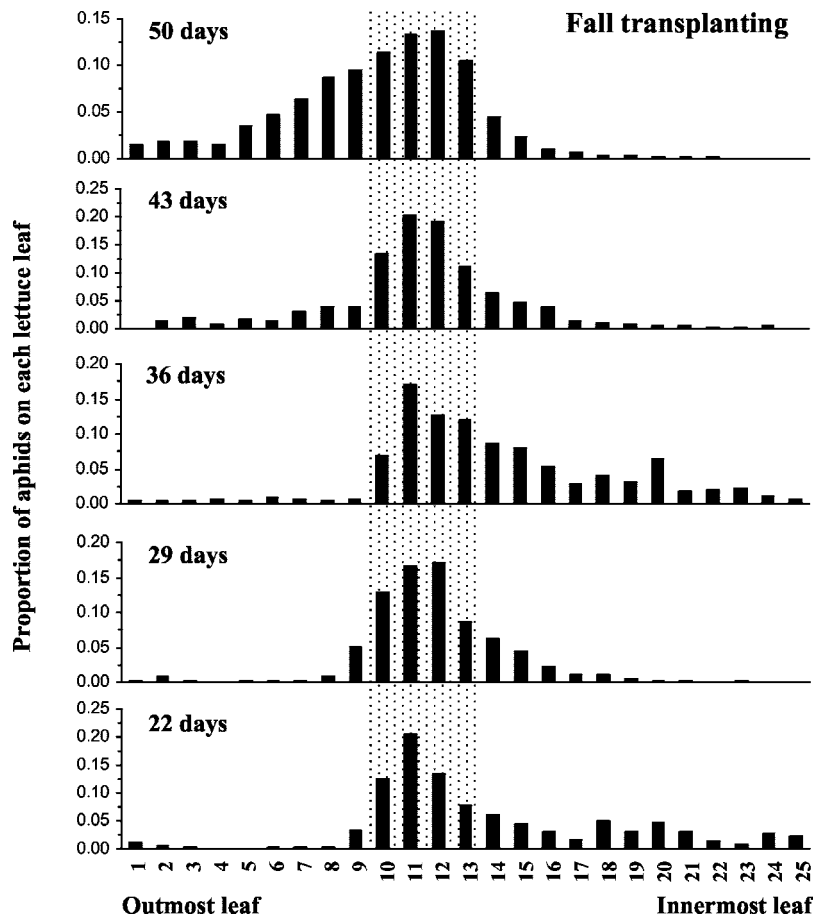


Fig. 2. Distribution of *N. ribisnigri* on leaves of iceberg lettuce plants for fall transplanting. Lettuce plants were transplanted on 23 September 2002 and harvested on 13 November 2002. The time period on each graph reflects the developmental time of the *N. ribisnigri* colony by the time of harvest. Leaves were numbered from the outermost frame leaf to the innermost head leaf inspected. Leaves in the shaded area are wrapper leaves.

on frame leaves increaseddramatically after 29 d of population growth for spring transplanting and after 36 d of population growth for fall transplanting. The proportion of the population on wrapper leaves showed relatively narrower ranges than proportions on frame or head leaves. The proportion of the population in lettuce heads tended to decline with developmental time, even though the absolute numbers of aphids in lettuce heads were still higher for longer developmental times given their larger population sizes (Table 1).

Aphid population density based on unit weight of plant tissue showed significant positive correlations with the proportions of the total population ( $y = 0.0848x + 0.0663$ ,  $R^2 = 0.5742$ ,  $P < 0.001$ ) and alates ( $y = 0.0917x + 0.2366$ ,  $R^2 = 0.4462$ ,  $P < 0.001$ ) on frame leaves (Fig. 3). As population density increased, larger proportions of *N. ribisnigri* populations were found on frame leaves. For all lettuce plants that were harvested 15–50 d after inoculation, both alates and apterous *N. ribisnigri* were found throughout the lettuce heads; no insect-free heads could be harvested.

The distributions of alates also shifted toward frame leaves as population density increased. Data from spring and fall transplanting showed similar distribu-

Table 1. Size and distribution of *N. ribisnigri* populations in iceberg lettuce plants over time

Time (d) <sup>a</sup>	n	Population size (mean ± SE)	Distribution (proportion)		
			Frame	Wrapper	Head
Spring transplanting					
43	3	4,057 ± 779	0.36	0.39	0.25
36	4	2,256 ± 389	0.15	0.52	0.33
29	4	1,284 ± 206	0.06	0.32	0.62
22	4	429 ± 113	0.02	0.17	0.81
15	4	287 ± 91	0.02	0.28	0.70
Fall transplanting					
50	3	4,184 ± 1,377	0.40	0.50	0.10
43	3	1,514 ± 404	0.18	0.62	0.20
36	3	1,320 ± 351	0.05	0.49	0.46
29	3	539 ± 67	0.10	0.69	0.21
22	3	212 ± 41	0.06	0.55	0.39

<sup>a</sup> Numbers of days after transplanting.

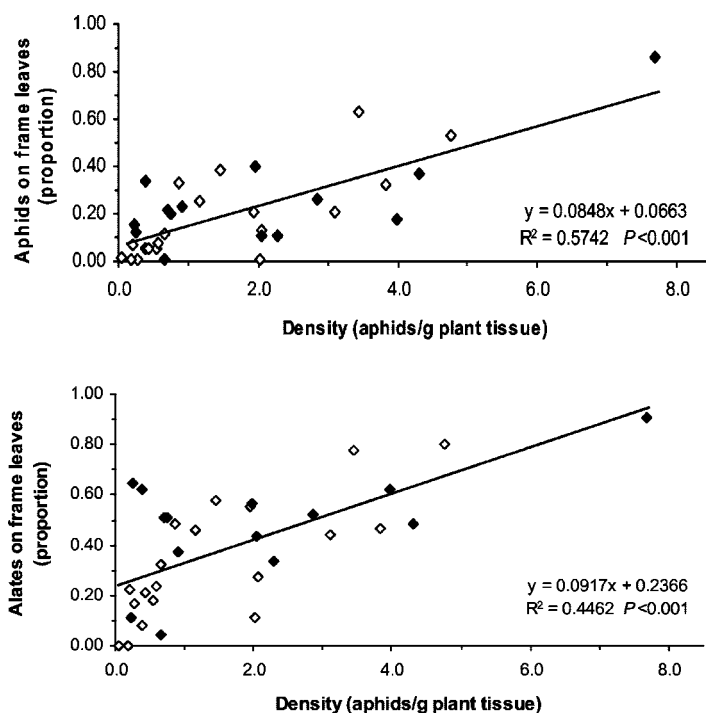


Fig. 3. Relationship between the proportion of total population on frame leaves and density of total populations of *N. ribisnigri* (top), and between the proportion of alates on frame leaves and density of alates (bottom) on individual caged lettuce plants. Open diamond represents spring transplanting and filled diamond represents fall transplanting.

tions and indicated consistency of populations shifting to frame leaves with increasing population density (Fig. 3).

There was no significant correlation between the population density and the proportion of alates ( $y = 0.0056x + 0.0975$ ,  $R^2 = 0.0376$ ,  $P = 0.280$ ), indicating that population density had no significant effects on alate production (Fig. 4). The average proportion of alates in the populations was  $\approx 10\%$ . There were, however, large variations in the alate proportion in *N. ribisnigri* populations especially at lower population densities. Data from the spring and fall transplanting showed similar distribution patterns. Therefore, the large variation in alate proportions was not due to the pooling of data from the spring and fall.

Logarithms of population sizes were significantly correlated with degree-days ( $y = 0.0039x + 1.623$ ,  $R^2 = 0.7915$ ,  $P < 0.001$ ), indicating that exponential aphid population growth could be predicted with increasing heat unit accumulation (Fig. 5). Data for spring and fall transplanting showed similar patterns of population growth in correlation with heat unit accumulation (Fig. 5). Based on the regression between logarithms of population size and heat unit accumulation, a 10-fold increase in population size required  $\approx 256$  DD above the  $5^\circ\text{C}$  developmental threshold.

Catches of *N. ribisnigri* alates on yellow sticky cards in the final week before harvest of lettuce plants had significant positive correlations with the total numbers of alates ( $y = 3.3144x + 72.208$ ,  $R^2 = 0.7535$ ,  $P < 0.001$ )

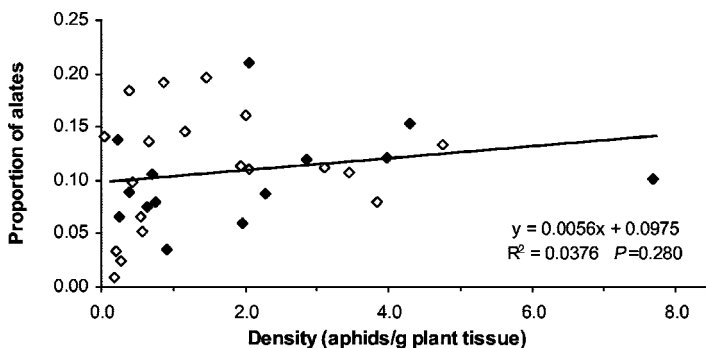


Fig. 4. Relationship between *N. ribisnigri* population density and proportion of the population as alates on individual caged lettuce plants. Open diamond represents spring transplanting and filled diamond represents fall transplanting.

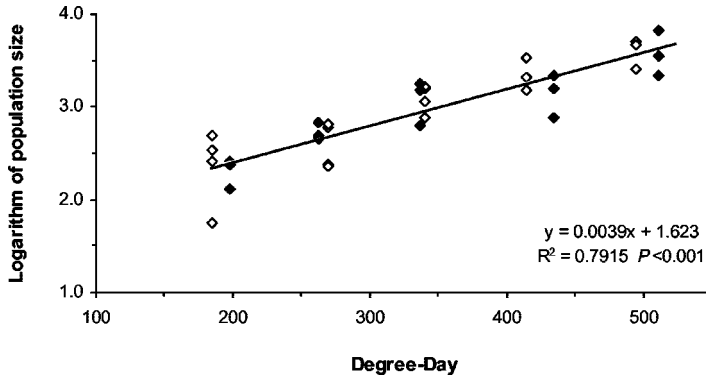


Fig. 5. Relationship between logarithm of population size of *N. ribisnigri* and degree-days accumulated ( $>5^{\circ}\text{C}$ ). Open diamond represents spring transplanting and filled diamond represents fall transplanting.

and the total population sizes of *N. ribisnigri* ( $y = 35.023x + 609.76$ ,  $R^2 = 0.7763$ ,  $P < 0.001$ ) on individual plants (Fig. 6). The most recent inoculations for the spring transplanting were excluded from the correlation analysis because no trap catch data for the final week were available. The intercept values of 72.2 and 609.8 for the regressions between the trap catch and alate, and between the trap catch and total population size, respectively, suggested expected sizes of the alate and total population when traps began to catch alates. These results indicate that even when there were no alates were caught on the yellow sticky cards, *N.*

*ribisnigri* may have developed large colonies and may have produced many alates that could disperse and infest other lettuce plants in the field.

### Discussion

Establishment of *N. ribisnigri* colonies from inoculations during 5 wk of plant development, from newly transplanted seedlings to the formation of lettuce heads, indicated that iceberg lettuce plants were susceptible to colonization by *N. ribisnigri* throughout their development. Consistent with results from a previous study (Mackenzie and Vernon 1988), *N. ribisnigri*

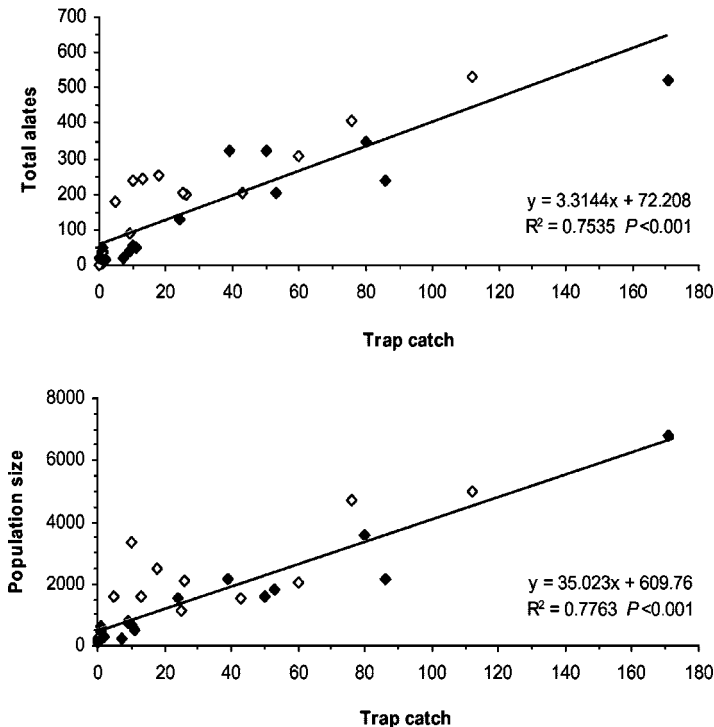


Fig. 6. Relationship between the catch of *N. ribisnigri* alates on yellow sticky cards and alate population size (top), and between alate catch and total population size (bottom), of *N. ribisnigri* on individual caged lettuce plants. Open diamond represents spring transplanting and filled diamond represents fall transplanting.



*gri* had higher population densities on wrapper leaves than on other leaves for most of the inoculated plants. The current study, however, also revealed that aphids were more concentrated inside heads in the early stage of population development and that the distribution shifted toward frame leaves as populations grew. The higher proportions of *N. ribisnigri* on head leaves than on frame leaves, for more recent inoculations, indicated that *N. ribisnigri* preferred the hearts of lettuce plants regardless of head formation. Formation of heads did not prevent colonization by *N. ribisnigri*. Within lettuce heads, leaf size was larger near the head surface and smaller near the center. Therefore, although most distributions of *N. ribisnigri* showed gradual declines from leaves near the head surface to leaves at the heart of the lettuce head (Figs. 1 and 2), the density based on unit weight of plant tissue may not decline on leaves near the heart of lettuce heads. The shift of the population distribution to frame leaves with increasing population density was likely due to crowding of aphids inside the heads caused by reproduction of the insect and diminishing space as heads become mature and compact.

The average size of  $\approx 4,000$  for a *N. ribisnigri* population on a single lettuce plant, with relatively long development time, was much larger than those ( $<1000$  per plant) reported on commercial lettuce (Mackenzie and Vernon 1988; Mackenzie et al. 1988; Palumbo 2000, 2003; Palumbo and Hannan 2002). Although large population sizes were estimated by partial counts of total aphids on leaf surfaces, the high correlations between population size and degree-day accumulation, and between population size and trap catch (Figs. 5 and 6), suggested that counting method did not introduce excessive bias to overestimate population size for plants with high aphid densities.

Unlike aphids on lettuce plants in the open field, aphids on caged plants in the current study could not disperse to other plants by flight of alates or crawling of wingless individuals. In the current study, *N. ribisnigri* populations were also allowed to develop for up to 43 and 50 d for the spring and fall transplanting, respectively. These long developmental times on single plants were not likely available for *N. ribisnigri* in commercial fields. Commercial iceberg lettuce plants in the Salinas Valley typically grow 65–70 d from planting to harvest. It usually takes 1 month to reach three- or four-leaf seedling stages after planting (Ryder 1999). Barrier effects of caging and long developmental times were likely to be the major causes of the extreme large population sizes on some plants. Other factors that may also contribute to the rapid population buildup were potential modification of microclimate by the cage and reduced mortality of aphids on caged plants to natural enemies. However, crowding and colonization of less preferred frame leaves also may hinder population growth.

For reasons discussed above, the population size on individual caged plants should not be expected on individual plants in the open field. Relevant to *N. ribisnigri* integrated pest management (IPM), however, population sizes on caged lettuce plants could be

considered as potential contributions of the introduction of only five individuals of *N. ribisnigri* to aphid population growth in the field. Population increase also may be projected based on the regression between logarithm of population size and heat unit accumulation. Accumulation of  $\approx 256$  DD above  $5^{\circ}\text{C}$  corresponded to a 10-fold increase in population size of *N. ribisnigri*. Because it was difficult to accurately measure aphid population growth rate in the field without caging host plants, due to insect dispersal, field cages still represented the best close-to-real field conditions for measuring insect population development (also see Hutchison and Hogg 1984). Therefore, the regression based on data from caged lettuce plants might still be valuable in gauging potential population growth rates of *N. ribisnigri* in the field. One major difference between a growth-rate projection by using these data versus open field population growth is the influence of natural enemies in commercial fields. Additional research on the potential for biological control of *N. ribisnigri* and effects of natural enemies on population growth rate should be done in commercial fields.

The proportions of alates in *N. ribisnigri* populations varied greatly among plants as indicated by the wide distribution deviating from the regression line (Fig. 4). This, and near zero slope of the regression line suggested that the proportion of alates did not depend significantly on population density. This result seemed to differ from findings in earlier studies with other aphid species. Crowding often causes increased production of alates to enable aphids to disperse as found in *Aphis fabae* Scopoli, *Megoura viciae* Buckton, *Rhopalosiphum padi* (L.), and *Sitobion avenae* (F.) (Dixon 1985). The difference between current findings and those in earlier studies with other aphid species might be because *N. ribisnigri* initially resided mostly in the hearts or inside heads of lettuce plants; large amounts of frame leaves are available to support growing *N. ribisnigri* populations. Although *N. ribisnigri* prefer the heart leaves of lettuce, the aphid also may grow and reproduce successfully on frame leaves as indicated by increased *N. ribisnigri* population density on frame leaves for plants with large *N. ribisnigri* population sizes. Given the existence of largely uncolonized frame leaves, it is possible that by the time of harvest, the highest density in our study may not have reached a critical level to induce production of disproportioned high numbers of alates if *N. ribisnigri* responded to crowdedness in the same as other aphid species.

It is not clear what influences the preference of *N. ribisnigri* for heart leaves. Differences in nutritional values or/and microclimate between frame leaves and heart leaves are potential causes. It is likely that microclimate on heart leaves in young lettuce plants, within lettuce heads, or under wrapper leaves are more stable with high humidity. Conversely, the microclimate on frame leaves are likely more arid and turbulent. *N. ribisnigri* reached the highest densities under wrapper leaves in contrast to low densities on adjacent frame leaves. It is likely that wrapper leaves

and the adjacent frame leaves were very similar except in microclimate. Therefore, the difference in microclimate may be an important factor for habitat preference of *N. ribisnigri* in lettuce plants. In addition, growing or senescent leaves have higher levels of soluble nitrogen in the phloem sap to support reproduction and growth of aphids than mature leaves (Dixon 1985). Therefore, it is also possible that heart leaves of lettuce are more nutritious than other leaves to *N. ribisnigri*, and this plays an important role in habitat preference by the aphid. It was unknown whether *N. ribisnigri* also might have behavioral preferences for heart leaves to avoid natural enemies.

Early detection of *N. ribisnigri* infestations is critical for its successful management. The significant correlations between trap catch and alate population size, and between trap catch and total population size, suggested that catches of alates on yellow sticky cards may provide a good indication on the level of *N. ribisnigri* infestations. However, the large values for the regression intercepts between trap catch and alate population size, and between trap catch and total population size, on individual lettuce plants (Fig. 6) suggested that when alates were caught on the traps, *N. ribisnigri* colonies were already well established. Therefore, it is doubtful that yellow sticky cards are useful for early detection of *N. ribisnigri* infestation in iceberg lettuce. The alternative for early detection of *N. ribisnigri* infestation is destructive sampling of lettuce plants. The concentration of *N. ribisnigri* inside heads when population size was small, as found in this study, suggests that destructive sampling is essential for early detection of *N. ribisnigri* in head lettuce.

Successful colonization of iceberg lettuce plants at different times during development, after single inoculations, indicates that lettuce plants are vulnerable to infestation by *N. ribisnigri* throughout their development. The high concentrations of *N. ribisnigri* in lettuce heads highlight the challenge in controlling *N. ribisnigri* with contact insecticides. These results provide additional evidence regarding the potential economic importance of *N. ribisnigri* and the need for research on alternative management strategies.

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